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QUANTIFY THE AIR FLOW AROUND AN
APPROACHING PREDATOR USING PIV

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1. EXECUTIVE SUMMARY

Wolf spiders hunt in the litter by moving at high speed, taking over unwary insect prey. Air flows generated ahead of hunting spiders can be a source of information for escaping prey. Crickets and numerous other arthropods possess extremely sensitive hairs that perceive the slightest air movements produced by approaching predators. The characterization of air displacements ahead of running arthropods was however never achieved. Here we provide full field digital particle image velocimetry measurements (DPIV) of air movements created in front of wolf spiders. We observed substantial air displacement in front of running spiders, noticeable at a distance of up to several centimeters. Our results have implications for attack strategies by predators and danger perception by prey. They most likely also apply to the large and diverse array of insect prey interacting with spiders in the litter.



2. QUANTIFY THE AIR FLOW AROUND AN APPROACHING PREDATOR USING PIV

2.1. INTRODUCTION

Near field fluid movement cues are used by a wide array of invertebrate animals to obtain information about potential predators, prey or mates, in both terrestrial and aquatic ecosystems. They are of major ecological and evolutionary importance, especially during predator-prey interactions as they directly influence the fitness of both partners. Despite the importance of near field fluid movement cues in many predator-prey interactions, their quantification upfront of moving predators has remained largely neglected. By contrast, near field fluid movements created by moving prey have been studied in great detail in several aquatic systems, from copepods to fishes. In particular, the flow in the wake of copepod prey and the use of the remaining trace in the fluid by their predator for homing on them was well studied. The situation is however strikingly different for spiders attacking insect prey on the ground. Wolf spiders, for example, pursue their prey at a very high speed on the bare soil and in the leaf litter. Crickets and many other herbivores and detritivores are thus subdued by these predators launching their fast strike by surprise. Air signals generated in front of running spiders can however be used by crickets for fast escape reaction. These insects are indeed fully equipped with air flow sensors, filliform hairs located at the rear end of their abdomen, which are among the most sensitive sensors known in the animal kingdom. In turn, spiders may use different strategies for hunting manoeuvres to cope with optimal air flow detection by crickets. Nearly nothing is known about air movements generated upfront by any running arthropod. The purpose of the present study was to quantify, with the use of digital particle imaging velocimetry (DPIV), the air flow upfront of a running spider, and to assess the importance of the observed air movement for attack strategies by predators and for escape strategies by prey.



2.2. METHODS

2.2.1. DPIV

We characterized the air flow generated by the spider displacement using the digital particle image velocimetry technique (DPIV). DPIV is a whole-flow-field technique providing instantaneous velocity vector measurements in a cross-section of a flow (Merzkirch 2001). The technique is mechanically (but not optically) non-intrusive and measures the velocities of micron-sized particles following the flow generated by the moving object in a laser sheet. Our measurement setup was composed of a sealed glass box (10 × 2 × 2 cm) (Figure 1), seeded with 0.2 μm oil particles (Di-Ethyl-Hexyl-Sebacat, 0.5 L, TPAS, Dresden, Germany) using an aerosol generator (ATM 230, ACIL, Chatou, France). The laser (NewWave Research Solo PIV 2, Nd:YAG, dual pulsed; Dantec Dynamics A/S, Skovlunde, Denmark) illuminated through the glass the flow produced by the spider displacement. The laser sheet (width = 17 mm, thickness at focus point = 50 μm) was operated at low power (3 mJ at 532 nm) to minimize glare. A target area (17 × 30 mm) was then imaged onto the CCD array of a digital camera (Photron FastCam X1280 PCI 4K) using a Macro Lens (Nikon, AF Nikkor, 60 mm, f : 2.8). Every 500 μs or 33 ms, the CCD captured a light pulse in separate image frames (1280 × 1024 px). Once a sequence of two light pulses was recorded, the images were divided into small subsections which are cross-correlated with each other using a flow map software (Flow Manager 4.4. Dantec Dynamics A/S, Skovlunde, Denmark). The correlation produced a signal peak, identifying the common particle displacement. An accurate measure of the displacement (and thus of the velocity), was achieved with sub-pixel interpolation. We obtained a velocity vector map of the air flow displaced by repeating the cross-correlation for each interrogation area over the two image frames captured by the CCD camera.

The RMS error of particle displacement is estimated at $\sigma_{pix} = 0.1$ pixel (Merzkirch 2001). This leads to a precision and hence the lowest detectable speed of $\sigma_v = 0.082$ mm/s if we use a time interval of 33 ms:

$$\sigma_v = \frac{\sigma_{\Delta x}}{\Delta_{time}} = \frac{\sigma_{pix} d_r}{\Delta_{time}}$$

with $\sigma_{\Delta x}$ the minimal displacement measurable (m), $\Delta_{time} = 33$ ms, the time separating two image record and $d_r = 27$ μm the spatial resolution. The same reasoning leads to a lowest measurable speed of 5.4 mm/s for a time interval of 500 μs.

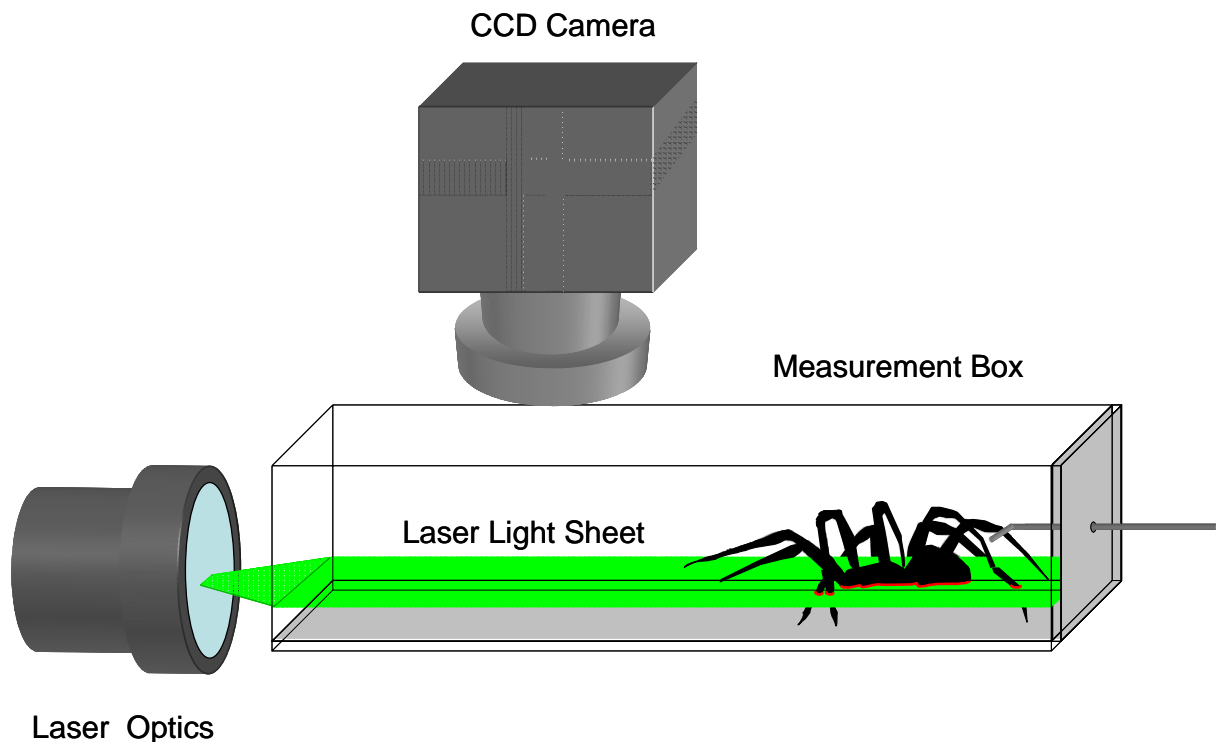
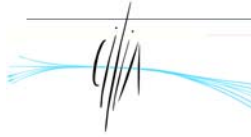


Figure 1: DPIV methodology. Spiders were gently forced to run in laser sheet positioned at body mid-height. The laser sheet is only 50 μm deep at the measurement point, so that air flow at the bottom is not considered.

2.2.2. Spider velocity estimation and profile extraction.

We obtained 22 measurements corresponding to 10 independent runs by 6 different *Pardosa* sp. spider individuals. Spider size ranged between 2.27 mm for the cephalothorax (N=6, S.D. 0.8) and over 1 cm with extended legs. Measurements were made only in those cases where the spider velocity was constant for several cm and spiders running straight. The spider velocity was determined by measuring the average velocity of the spider body on a complete run. For each measurement we extracted velocity profiles from the vector fields. Profiles were taken in the front of the spider head. We extended the time between two images to 33 ms to measure very low velocities, disabling thereby measurement within the first 5 mm in front of the body for a speed of 15 cm/s. We observed an offset velocity at large distance, which origin may lie in the movement created while triggering the spider, and which we subtracted to each profile separately. Its estimation was done in taking a 3 points mean value between the distances 23 mm and 24 mm. While the spiders mean velocity is in the range of values observed during attacks, we were not able to let them run at some of the high speed observed in reality. We do not know whether the 'escape' runs do differ in terms of leg and body kinetics from attack runs.



2.3. RESULTS

The mean velocity of spiders was 11.3 cm/s (SD = ± 7.3 , N= 22), within the range of attack speeds observed under unconstrained hunting behaviour. Running spiders displaced air in front and above themselves. Regions of high velocity near the moving legs could be observed (Figure 2), but they did not last for long (Figure 3).

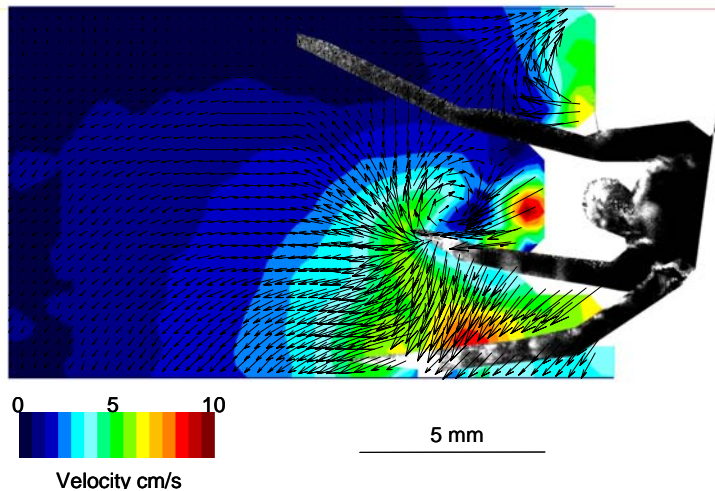


Figure 2: Close-up of the spider's front (three legs) and flow field velocity produced by leg movements. The arrows represent the velocity direction and magnitude, and the color a smoothed velocity gradient.

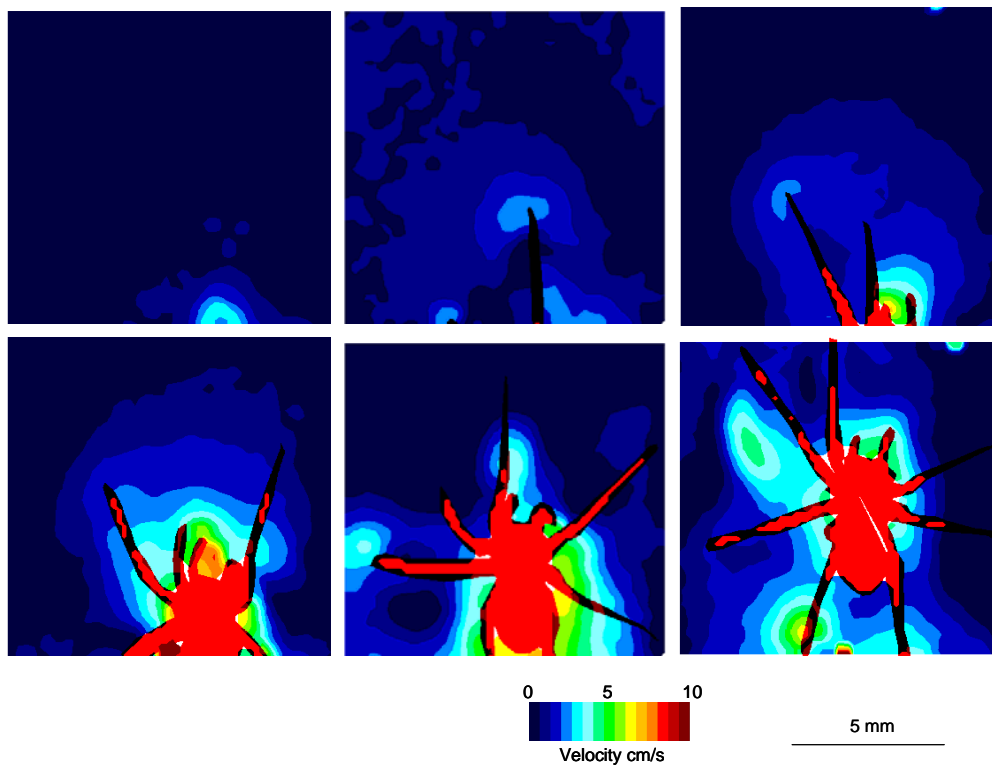




Figure 3: Flow field of a running spider. This sequence highlights the pockets of high but transient velocity created by leg strokes and the lasting air movements created by the body trunk movement. The tip of the spider's legs, nor their associated vortex, are visible as they are situated below the light sheet. The time delay between two images is 500 μ s.

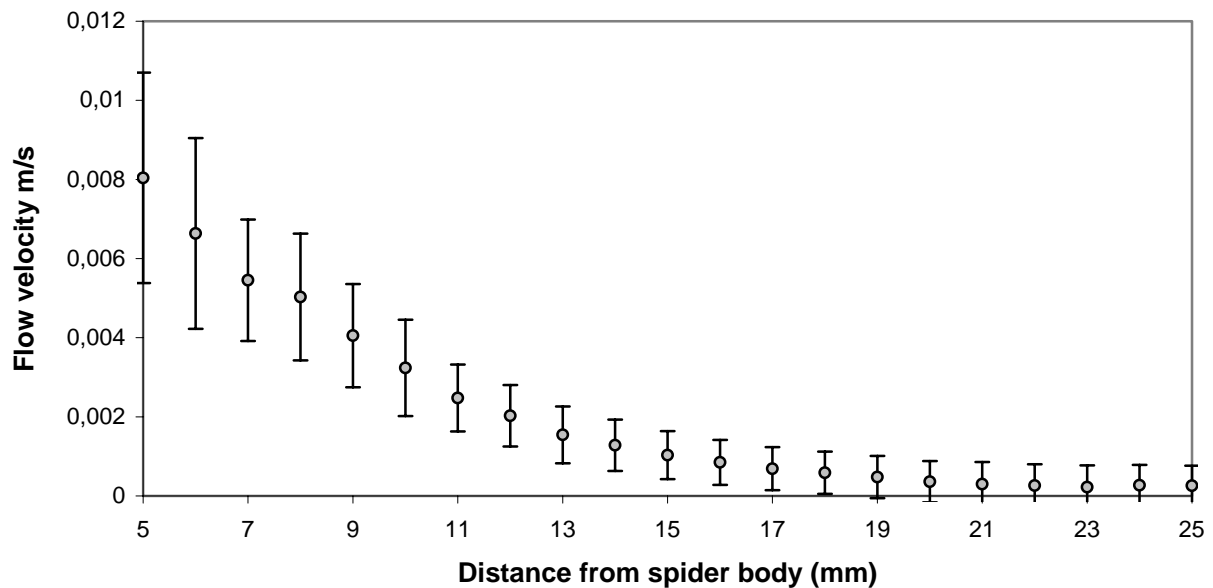


Figure 4: Flow velocity along a transect upfront of running spiders (mean and standard deviation). The increased error near the spider body is due to a declining number of records. The time interval between two images was 33 ms.

The Reynolds number of a spider running at the observed mean speed is therefore around 20. Hunting spiders are known to be able to walk at low and high speed too, so that the observed lowest and highest speeds (up to 40 cm/s) lead to Re numbers ranging from 6 to 60.

2.4. CONCLUSION

The observed flow pattern has implications for perception and escape strategies in prey and for attack strategies in predator. The air field is strongly disturbed by a running spider. Prey may tap into this unwanted information to identify danger and to take appropriate escape decisions. We use crickets and cockroaches here as an example of prey, as the neural and biomechanical processes of their cercal escape system has been worked in detail and has long attained the textbook status. The qualitative nature of the observed flow, a time dependent laminar flow similar to a ramp, is markedly different from the one usually assumed, even though Rinberg and Davidowitz (2003) did assume the proper qualitative form of the stimulus. Oscillatory, burst and jet stream are usually used for experimental works. All models of filiform hair biomechanics and cercal functioning, as well as a great majority of experimental work, assume and use oscillatory flows. This type of flow is produced by hunting flying wasps as predator signals. These predators have been reported in the natural



history and the neuroethological literature. It is only very recently that the first quantitative field study on mortality factors on wild crickets identified *Pardosa* wolf spiders as being the largest mortality factor in the wood cricket *Nemobius sylvestris*.

2.4.1. Implications for prey strategy

Our results suggest that a cricket recognizes an incoming danger in the successive recruitment of hairs of decreasing size triggered only once. Previous work indeed showed that the very sensitive long hairs (>1000 microns) are velocity sensors while the short hairs are acceleration sensors with a length dependent sensitivity threshold (Kanou & Shimozawa 1984). The hair movement during an attack and the computational basis of the cercal system should be revisited according to the qualitative aspect of flow produced by the different types of cricket predators. Our results, combined with previous knowledge on single hair biomechanics can also permit us to make rough predictions about the maximal perception distance of an approaching predator. The smallest velocity at which a single hair does fire is $V_{\text{thresh}} = 30 \mu\text{m/s}$. The precision of our measurements is however limited to some $80 \mu\text{m/s}$. The observed decline in flow velocity (Figure 4) implies that this threshold is attained around 2 cms in front of a spider. We never observed such large distances in field trials with wild crickets, which escaped at a distance between ca. 4 mm and 10 mm (Dangles et al. 2007). Information processing in the abdominal terminal ganglion and possibly in the insect brain, as well as processes related to leg movements do take time and may be the reason for the differences between perception at the hair level and escape decision at the organism level.

2.4.2. Implications for predator strategy

Our results may explain the two attack strategies we observed in this group of spiders (Dangles et al. 2006). Spiders do attack prey either by extremely slow motion corresponding almost to a sit and jump strategy, and of blazing speed (up to 40 cm/s). Intermediate speeds are much less frequent and biotests using a piston mimicking the attack of a spider showed that crickets' survival was highest at 20 cm/s. Almost no information is conveyed through fluid movement in the first case. In the second case, the attack speed is such that the prey receives a lot of information it cannot really use, as the spider is simply too quick.

Spiders were among the first invertebrate predators on land, long before predatory beetles and wasps appeared. Their predation pressure on herbivores and detritivores has been an enduring one and many prey living in the litter harbour well developed cerci bearing filliform hairs triggered by slightest air movements. These include primitive and modern insects such as bristeltails, firebrats, springtails, cockroaches and crickets, most still caught in the same interaction with spiders today, some 400 millions years later. In the meantime, a vast array of additional invertebrate predators hunts them in the way spiders do, from several other arachnid groups to carabid, cincidelid and staphylinid beetles. Our results imply that the air movements generated by these predators should not greatly differ from the relationship we quantified: speed, body trunk size and maybe height above ground are all what matters. Lurking predators may hide and wait for most of the time, but the final strike does produce unavoidable signals prey exploit for their very survival.



2.4.3. Remaining work

The most urgent work is to have a better grasp at the physics behind Figure 4, which is highly composite. The role of the transient pockets of high velocities produced by legs must be assessed. We are currently tackling this task by running experiments with spheres of varying diameters and speeds, analytical approximations (potential and viscous flow) as well as numerical solution of the full Navier-Stokes equation. Finally, the sensitivity of our results to spider speed is in need of clarification.

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